

THE BIOLOGY OF MILESIA RUSTS

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With plates 84 to 86

AS PART of a contribution towards a monograph on *Milesia* I have recently presented an account of the taxonomy and geographical distribution of the species of this genus (2). The paper now offered, the third of a series on the Pucciniastreae, is devoted, except for a short section on economic considerations, to topics on the biology of Milesian rusts. These topics comprise (1) hosts, (2) life history studies, (3) developmental periods, (4) habits of spore production, (5) host restrictions.

HOSTS

Ferns and ferns only serve as hosts for the diploid generation of all known species of rusts belonging to the genus *Milesia*. These are representatives of about sixteen genera scattered among various subfamilies of the one family, the Polypodiaceae. This limitation is an interesting phenomenon the significance of which can only be conjectured because the Polypodiaceae are regarded as the most recent family of homosporous Filicales. The genera and the subfamilies to which they belong are as follows: ACROSTICHEAE - *Elaphoglossum*; ASPIDIEAE - *Dryopteris*, *Polystichum*; ASPLENIEAE - *Asplenium*, *Blechnum*, *Diplazium*, *Scolopendrium*; DAVALLIEAE - *Nephrolepis*, *Odontosoria*; POLYPODIEAE - *Drynaria*, *Polypodium*; PTERIDEAE - *Coniogramme*, *Cryptogramma*, *Histiopteris*, *Pellaea*; WOODSIEAE - *Dennstaedtia*. Lacking from the list are but the two small subfamilies VITTARIEAE and OLEANDREAE.

In addition to the fact that the fern hosts compiled above are all polypodiaceous they are characterized in common by the general habit of "overwintering" some of their fronds in a more or less green condition. Recognition of this feature is important both to the collector and the student of Milesian rusts. This fact is emphasized because associated with it is the postponement beyond the current season, typical of so many species, of the formation of teliospores; they develop with exceptions in the spring on overwintered, affected fronds. Associated also is the production of crops of uredospores (often the most prolific)

in the spring on the overwintered, affected fronds. The latter phenomenon explains how it is that a species of *Milesia* may be perpetuated indefinitely without the necessity of teliospores and a haploid stage; it likewise provides a basis for a reasonable understanding of the world-wide distribution and the course of evolution beyond the range of the one known generic alternate host of this remarkable group of rusts.

Alternate hosts have been more or less satisfactorily determined for ten (nine if *M. fructuosa* is the same as *M. intermedia*) species of *Milesia*, and in every instance they have proved to be species of *Abies*. Heretofore no consistent effort has been made to discover how many species of *Abies* might be susceptible to any one particular species of *Milesia*. But as Klebahn (7) found that *A. alba* and *A. cephalonica*, the only ones he tested, served as hosts for *M. Blechni*, and Kamei (4) found that *A. Mayriana*, *A. firma* and *A. sachalinensis*, the only ones he tested, served as hosts for *M. exigua*, there appeared to be ground for anticipating that host restrictions are not prevalent in firs to anything like the same extent as in ferns. The results of experiments recorded in this paper in which *M. fructuosa* was tested out on a wide range of fir species add confirming evidence to this supposition. In addition to the nine or ten species whose alternate hosts are known there are approximately fifteen species whose teliospores have been described but for which as yet the haploid stage remains to be discovered. All but one of these occur within the range of *Abies*; they include such well-known species as *M. murariae*, *M. Feurichii*, *M. Polystichi*. It is almost certain that they, too, pass to *Abies*. Regarding the remainder of the species, those for which uredospores only are known, any from north temperate regions, such as *M. Magnusiana*, doubtless produce teliospores and likely have *Abies* as alternate host. Naturally there is uncertainty regarding the haploid hosts of those species that are restricted to areas beyond the range of *Abies*. As a matter of fact our acquaintance with such species is still so limited that we know of the existence of teliospores in but the one species, *M. australis*. Elsewhere (2) I have advanced the hypothesis that at least some of the Milesian species of the tropics, subtropics and Southern Hemisphere may be imperfect species, evolutions from the diploid phase of perfect species and perpetuated solely by means of uredospores. In any case it is clear that a great deal of fascinating observation and experimentation remains to be done on host relationships of a large proportion of the species of *Milesia*.

LIFE HISTORY STUDIES

The first successful study of the complete life history of any species of *Milesia* was made by Klebahn (7); the species studied was *M. Blechni* (Syd.) Arthur. Professor Klebahn employed as primary inoculum telial material from overwintered fronds of *Blechnum Spicant* (L.) With. collected in the spring of the year. At various dates between May 16 and June 5, 1915, portions of the inoculum were suspended over small potted plants of *Picea Abies* (L.) Karst., *Abies alba* Mill. and *A. cephalonica* Loud.; these were then covered by bell jars and kept covered for as long as six days. *Picea* remained free from infection; but on *Abies* evidences of aecial formation began to appear June 21 on the earlier inoculated plants, and the first mature aecia were observed July 10, or 55 days after the experiment was started. This interval may be taken as an approximately correct measure of the developmental period of the rust on *Abies*, for while it would actually be shorter at least by the time that elapsed between the setting of the inoculum in place and the shedding of the basidiospores, yet this could not have been more than a few days at most because the inoculating material in any instance was not in use for more than six days. All of the experimental plants of both species of *Abies* produced a copious crop of aecia, but on needles of the current season only. Some of the aecial-bearing needles were distributed in Jaap's Fungi selecti exsiccati under number 774a; the remainder were used for the inoculating of ferns of the species *Blechnum Spicant* (L.) With., *Dryopteris spinulosa* (O. F. Müller) Kuntze and *Scolopendrium vulgare* Smith.

The ferns were inoculated at various dates beginning July 20. A marked degree of infection resulted on *Blechnum*, the plants first inoculated showing clear indications of rust along in August; the developmental period in all instances was protracted. No mention was made of any signs of infection on *Dryopteris*. Injuries were observed on *Scolopendrium*, but their cause was not determined; somewhat similar injuries on *Blechnum* were ascribed to the effects of manipulation of the fronds during the course of the experiment. These cultures were supplemented by others in which uredospores from pustules on overwintered fronds of *B. Spicant* were transferred under suitable conditions to new, healthy fronds of the same species; the results were positive. Thus, inoculations made June 21 were followed by the production of uredinia which began to sporulate July 12, indicating a developmental period of three weeks. Summarizing, Klebahn established the outstanding facts that *Abies*, equally true for both species tested, serves as the alternate

host of *Milesia Blechni*, and that this rust is capable of perpetuation from year to year on its fern host alone without the alternation of the aecial stage.

Life history studies of certain other species of *Milesia* have been reported more recently by Faull (2) and by Kamei (4, 5, 6); in addition, Dr. Eugène Mayor informs me that he has obtained uredinia of *M. Kriegeriana* (Magnus) Arthur by sowing aeciospores of a white-spored *Peridermium* on fronds of *Dryopteris spinulosa* (O. F. Müller) Kuntze, but his publication has not yet appeared.

To Kamei we owe accounts of determinations of the host interrelationships of *Milesia exigua* Faull (*Milesina vogesiaca* Kamei, not Sydow), *Milesia jezoensis* (Kamei) Faull, *M. Miyabei* (Kamei) Faull

The telial materials of *M. exigua* with which Kamei initiated his studies (4) of that species were collected in the fall from fronds of the current season of *Polystichum Braunii* (Spenner) Fée. They were placed in cotton bags and hung on the shady side of a wall to overwinter. The following spring, at the time the new leaves of *Abies* were unfolding, portions of the fronds carrying teliospores were placed in Petri dishes lined with moist paper and kept there until basidia began to emerge—an interval of two or three days as it proved to be. The pieces so treated were next placed on the foliage of potted firs freshly sprayed with water, and all covered with bell jars for two or three days. After the bell jars were removed the inoculated firs were transferred to a cool place and watered daily. In the course of his experimentation three species of *Abies* were tested, namely, *A. Mayriana* Miyabe & Kudo,¹ *A. sachalinensis* Mast. and *A. firma* Sieb. & Zucc. Infection resulted in all three species and in the new needles only. Spermogonia appeared in from 13 to 20 days following inoculation, and aecia in from 21 to 28 days. Six out of nine tests on *A. Mayriana* were successful, one (spermogonia only) out of three on *A. sachalinensis* and one out of two on *A. firma*. From aecia that formed on *A. Mayriana* and *A. firma* one sowing of aeciospores each was made on fronds of *P. Braunii*, the first on pinnae of a potted plant, the second on detached pinnae in a Petri dish. Uredinia developed within 17 and 13 days respectively. While we might wish that the data were more voluminous we can unreservedly accept Kamei's conclusion that *M. exigua* alternates between *Abies* (three species tested) and *P. Braunii*.

Milesia jezoensis was the next species studied by Kamei (5). Telial

¹*Abies Mayriana* is often considered a variety of *A. sachalinensis* - *A. sachalinensis* var. *Mayriana* Miyabe & Kudo.

material was collected in the spring on overwintered fronds of *Polypodium vulgare* L. The portions to be employed as inoculum were placed in a moist chamber and left there until basidia could be detected—a period of two or three weeks. Just what the unexpected length of this interval means is not clear, that is, whether the teliospores were immature at the time of collection or that in this species they require a resting period before germination will take place or that the early growth of the basidia is exceptionally slow or that conditions suitable for immediate rapid growth were not provided. As soon as the basidia emerged the inoculum was suspended over the foliage of small, potted trees of *A. Mayriana* on which the new needles had recently expanded, the same technique being employed as for *M. exigua*. Four out of nine tests were successful, and in these spermogonia appeared on needles of the current season only and within about 20 days. For some reason, probably because of poor condition of the firs, no aecia developed and most of the infected needles dropped before the end of the summer. Naturally because of the lack of aeciospores inoculations in the opposite direction, that is, from *Abies* to *Polypodium*, were impossible. While the incompleteness of this experimentation and the paucity of data obtained call for a repetition of the work, yet Kamei's conclusion as to the host connections of *M. jezoensis* may be reasonably accepted as correct.

Kamei has likewise reported (6) partial life history studies of *M. Miyabei* and *M. Dryopteridis*, but his published data on these are particularly meager. For both species the telial materials employed as inocula were collected on overwintered fronds—on *Dryopteris crassirhizoma* Nakai for *M. Miyabei* and on *M. viridescens* (Bak.) Kuntze for *M. Dryopteridis*. Inoculations were made on *Abies Mayriana* and in due course lesions appeared, but on the new needles only. Eventually these bore spermogonia and aecia in the case of *M. Miyabei*, but spermogonia only in the case of *M. Dryopteridis*. For the latter the developmental period up to the production of spermogonia was about 38 days; no time records were given for *M. Miyabei*. Here again, while the results warrant the reasonable conclusion that *A. Mayriana* may carry the haploid stage of *M. Miyabei* and *M. Dryopteridis*, fuller and more complete data are desired.

My own researches have pertained to the species *Milesia intermedia* Faull (probably a condition of *M. fructuosa* Faull in which the uredinia are omitted or if present at all are much reduced), *M. fructuosa* Faull, *M. marginalis* Faull and Watson, and *M. polypodophila* (Bell)

Faull. These were conducted during the summers of 1924-7 at the University of Toronto Field Laboratory of Forest Pathology located on Bear Island, Lake Timagami, Timagami Forest Reserve, Ontario, and during the summer of 1933 at the Arnold Arboretum, Harvard University, Jamaica Plain, Mass. In the former locality all these rusts are readily obtainable in ample quantities on their fern hosts; and their coniferous host, *Abies balsamea* (L.) Mill., abounds. In the latter locality neither the fern hosts nor spontaneous plants of *Abies* occur; the material used as inoculum was collected on ferns in the Berkshire Mountains of western Massachusetts, and the firs inoculated were trees that at one time or another had been planted in the Arboretum.

Studies on each of the species began with the telial stage. At the time the new needles of *Abies* were expanding overwintered fronds bearing teliospores were brought into the laboratory, and, so as to force spore germination, they were placed between folds of wet paper or laid on damp sphagnum moss in large loosely covered cans. Small test pieces were also kept under moist conditions in Petri dishes to afford greater ease of observation. Close watch was kept for the emergence of basidia and the first formation of basidiospores. As soon as basidiospores were freely appearing the material was ready for making inoculations. In setting up an experiment a portion of a frond carrying inoculum was either laid, abaxial surface down, directly on the foliage of a small branch of the host to be inoculated, or it was first prepared for easier handling and greater economy in use by laying it between two strips of galvanized wire netting, separated from the upper strip by a piece of wet absorbent paper. The chosen branch by way of its preparation was sprayed with water from an atomizer and so flexed that its lower face would come in juxtaposition with the basidial-bearing face of the piece of frond. A celluloid cylinder about six inches long by two inches in diameter (E. E. Hubert—Celluloid cylinders for inoculation chambers. *Phytopath.* 6:447-450. 1916) plugged at one end with wet sphagnum was then slipped over the branch and its adjustment completed by packing its proximal end around the branch in its axis with wet sphagnum. Whenever necessary the branch was propped to keep it as nearly as possible in a horizontal position until the tube was finally removed some days later. The experiment was visited daily as long as the tube was in use, and the sphagnum plugs were kept wet by the addition of water as needed. Similar technique was employed in subsequent inoculations of ferns except that the inoculum consisted of a suspension of spores in water which was sprayed on the fronds.

TABLE 1. *Milesia intermedia*—
from *Dryopteris spinulosa intermedia* to *Abies balsamea*

Date of inoculation	First appearance of lesions	First appearance of spermatogonia	First appearance of peridermia	Date harvested	No. of needles infected	No. of needles with peridermia
27. vi.24	14 days	—	36 days	40 days	50	33
27. vi.24	14 "	—	36 "	40 "	100	80
27. vi.24	14 "	—	34 "	45 "	150	140
27. vi.24	14 "	—	34 "	40 "	90	80
28. vi.24	13 "	—	35 "	39 "	32	26
28. vi.24	13 "	—	33 "	39 "	24	21
28. vi.24	12 "	—	33 "	41 "	100	90
28. vi.24	12 "	—	33 "	41 "	90	80
28. vi.24	12 "	—	33 "	39 "	100	80
4.vii.27	14 "	16 days	34 "	43 "	—	2
4.vii.27	13 "	15 "	38 "	43 "	—	4
4.vii.27	13 "	15 "	34 "	43 "	—	8
4.vii.27	19 "	19 "	34 "	43 "	—	5
4.vii.27	19 "	21 "	37 "	43 "	—	5
4.vii.27	13 "	19 "	32 "	43 "	—	13
4.vii.27	13 "	19 "	34 "	43 "	—	15
4.vii.27	—	—	34 "	43 "	—	3
4.vii.27	16 "	19 "	35 "	43 "	—	7
5.vii.27	15 "	20 "	34 "	45 "	—	10
5.vii.27	13 "	18 "	34 "	45 "	—	17
5.vii.27	13 "	20 "	34 "	45 "	—	17
5.vii.27	18 "	20 "	34 "	45 "	—	8
5.vii.27	10 "	20 "	36 "	45 "	—	5
5.vii.27	18 "	18 "	37 "	45 "	—	7
5.vii.27	18 "	20 "	—	—	—	0
6.vii.27	17 "	17 "	33 "	45 "	—	13
6.vii.27	11 "	14 "	33 "	45 "	—	11
6.vii.27	11 "	14 "	33 "	45 "	—	23
6.vii.27	11 "	17 "	36 "	45 "	—	2
6.vii.27	14 "	17 "	33 "	45 "	—	5
6.vii.27	12 "	17 "	33 "	45 "	—	16
Averages	14 "	18 "	34 "			

Average no. of peridermia per needle bearing peridermia—7.

Peridermia ruptured in from 1 to 6 days or an average of about 3 days.

No. of controls examined 74 to 152.

One experiment without infection.

Percentage of needles infected varied from 1 to 33.

All of the experiments were conducted out-of-doors. Two sets of experimental plants were used in the Timagami experiments, one set consisting of well-established potted plants located in a protected "garden" where natural infection was altogether unlikely (in our experience none ever occurred) and under as nearly normal conditions as possible; and a second set consisting of undisturbed plants in a favorable natural habitat, in localities well removed from occurrences of Milesian rusts. The latter set likewise remained free from natural infections. In the Arnold Arboretum experiments the undisturbed trees scattered about the Arboretum were used; an auxiliary set was not necessary because these trees are entirely free from Milesian rusts and far removed from any possible source of spontaneous infection. Uninoculated branches and uninoculated plants in the immediate neighborhood served as controls. Data on the experiments are assembled in Tables 1-7.

TABLE 2. *Milesia intermedia*—
from *Abies balsamea* to various ferns

Fern inoculated	Date of Inoculation	Date Harvested	Results
<i>Dryopteris spinulosa intermedia</i>	12.viii.24	5.vi.25	III
" " "	16.viii.27	27.vi.28	III
" " "	12.viii.24	5.vi.25	III
" " "	24.viii.24	5.vi.25	III
<i>Dryopteris spinulosa</i>	16.viii.27	30.vi.28	III
" "	12.viii.24	5.vi.25	III
<i>Dryopteris marginalis</i>	16.viii.27	30.vi.28	No infection
" "	19.viii.27	28.vi.28	" "
" "	19.viii.27	28.vi.28	" "
" "	19.viii.27	28.vi.28	" "
" "	20.viii.27	27.vi.28	" "
<i>Dryopteris cristata</i>	16.viii.27	28.vi.28	No infection
<i>Dryopteris fragrans</i>	20.viii.27	29.vi.28	No infection
" "	20.viii.27	29.vi.28	" "
" "	20.viii.27	29.vi.28	" "
" "	20.viii.27	29.vi.28	" "
" "	20.viii.27	29.vi.28	" "
<i>Polystichum acrostichoides</i>	16.viii.27	27.vi.28	No infection
" "	19.viii.27	27.vi.28	" "

The aeciospores used as inoculum were produced in the experiments recorded in Table 1.

TABLE 3. *Milesia marginalis*—
from *Dryopteris marginalis* to *Abies balsamea*

Date of inoculation	First appearance of lesions	First appearance of spermatogonia	First appearance of peridermia	Date harvested	No. of needles infected	No. of needles with peridermia
27. vi.24	13 days	—	47 days	53 days	180	160
25. vi.24	21 "	—	51 "	55 "	14	14
25. vi.24	19 "	—	51 "	55 "	25	25
27. vi.24	13 "	—	42 "	53 "	150	130
27. vi.24	13 "	—	42 "	53 "	21	20
27. vi.24	13 "	—	42 "	55 "	400	310
28. vi.24	13 "	—	46 "	54 "	170	130
28. vi.24	13 "	—	46 "	52 "	380	270
28. vi.24	13 "	—	46 "	52 "	250	190
28. vi.24	13 "	—	41 "	52 "	200	170
28. vi.24	13 "	—	41 "	52 "	290	250
28. vi.24	13 "	—	41 "	52 "	190	140
28. vi.24	13 "	—	43 "	54 "	330	260
28. vi.24	13 "	—	41 "	52 "	55	50
28. vi.24	13 "	—	41 "	52 "	260	210
29. vi.27	12 "	18 days	40 "	54 "	—	105
29. vi.27	18 "	18 "	45 "	54 "	—	8
29. vi.27	14 "	19 "	43 "	54 "	—	19
29. vi.27	12 "	18 "	42 "	54 "	—	58
29. vi.27	12 "	18 "	43 "	54 "	—	21
29. vi.27*	12 "	18 "	39 "	54 "	—	106*
29. vi.27	12 "	18 "	39 "	54 "	—	87
29. vi.27	14 "	19 "	40 "	57 "	—	52
29. vi.27	14 "	19 "	42 "	57 "	—	77
29. vi.27	12 "	19 "	42 "	57 "	—	26
29. vi.27	14 "	19 "	42 "	57 "	—	57
29. vi.27	12 "	18 "	42 "	57 "	—	83
29. vi.27	14 "	18 "	45 "	57 "	—	26
29. vi.27	12 "	19 "	45 "	57 "	—	41
30. vi.27	18 "	23 "	42 "	57 "	—	40
30. vi.27	18 "	21 "	44 "	57 "	—	43
30. vi.27	15 "	23 "	42 "	57 "	—	51
5. vii.27	12 "	20 "	39 "	52 "	—	21
5. vii.27	14 "	20 "	45 "	52 "	—	3
5. vii.27	12 "	20 "	45 "	52 "	—	4
5. vii.27	12 "	20 "	40 "	52 "	—	29
5. vii.27	12 "	20 "	41 "	52 "	—	25
5. vii.27	12 "	20 "	41 "	52 "	—	34
Averages	14—"	19+"	43 "			

Material was ready for inoculation one day after collection.

Average no. of peridermia per needle bearing peridermia—7.

Peridermia ruptured in from 1 to 8 days or an average of about 4 days.

No. of controls 54 to 1114.

Four experiments without infection.

Percentage of needles infected varied from 2 to 65, an average of 33%.

Percentage of needles infected when inoculation was at best, an average of 40%.

*Plates 84 and 85 are photographic records of this experiment.

TABLE 4. *Milesia marginalis*—
from *Abies balsamea* to various ferns

Fern inoculated	Date of Inoculation	Date Harvested	Results
<i>Dryopteris marginalis</i>	20.viii.24	22.vi.25	II, III abundant
" "	20.viii.24	5.vi.25	II, III "
" "	24.viii.24	5.vi.25	II, III
" "	22.viii.27	27.vi.28	II, III very abundant
" "	22.viii.27	27.vi.28	II, III abundant
" "	25.viii.27	28.vi.28	II, III abundant
" "	25.viii.27	28.vi.28	II. Frond injured by an animal
" "	26.viii.27	28.vi.28	II, III
" "	26.viii.27	29.vi.28	II, III abundant
<i>Dryopteris cristata</i>	23.viii.24	22.vi.25	No infection
" "	23.viii.24	22.vi.25	" "
" "	23.viii.24	22.vi.25	" "
" "	23.viii.24	22.vi.25	" "
" "	22.viii.27	28.vi.28	" "
" "	25.viii.27	28.vi.28	" "
<i>Dryopteris fragrans</i>	25.viii.27	29.vi.28	No infection
" "	25.viii.27	29.vi.28	" "
" "	27.viii.27	29.vi.28	" "
" "	27.viii.27	29.vi.28	" "
<i>Dryopteris spinulosa</i>	23.viii.24	22.vi.25	No infection
" "	22.viii.27	29.vi.28	" "
" "	22.viii.27	30.vi.28	" "
" "	25.viii.27	27.vi.28	" "
<i>Dryopteris spinulosa intermedia</i>	20.viii.24	22.vi.25	No infection
" " "	20.viii.24	22.vi.25	" "
" " "	22.viii.27	27.vi.28	" "
<i>Polypodium virginianum</i>	25.viii.24	22.vi.28	No infection
" "	25.viii.24	22.vi.28	" "
<i>Polystichum acrostichoides</i>	22.viii.27	27.vi.28	No infection
" "	25.viii.27	27.vi.28	" "
" "	26.viii.27	27.vi.28	" "

The aeciospores used as inoculum were produced in the experiments recorded in Table 3.

TABLE 5. *Milesia polypodophila*—
from *Polypodium virginianum* to *Abies balsamea*

Date of inoculation	First appearance of lesions	First appearance of spermogonia	First appearance of peridermia	Dates of harvest
21.vi.24	Summer of 1926	June, 1927	25.vii.27 (on needles of 1924)	7.viii.28 (needles of 1924-5) (Herb. #8597)
21.vi.24	Summer of 1926	June, 1927	25.vii.27 (on needles of 1924)	25.viii.28 (needles of 1923-5) (Herb. #8596)
21.vi.24	Summer of 1926	June, 1927	19.vii.27 (on needles of 1924)	28.vii.27 (Herb. #8380) 12.vii.28 (needles of 1924-5) (Herb. #8598)

The telial material of *M. polypodophila*, on overwintered fronds of *Polypodium virginianum*, was collected June 19, 1924. The fronds were placed at once in a moist chamber. There was an abundance of basidiospores in evidence two days later, and that same day, June 21, fourteen experiments were set up. The inoculated plants were closely examined from time to time during the remainder of the summer, but no signs of infection could be detected. Likewise, during 1925 there were no obvious signs of infection; but some needles were perhaps very slightly paler than others; an examination of a few of these revealed the presence of mycelium. By midsummer of 1926 needles on some of the experiments were more certainly paler and samples of these were found to contain mycelium. During the winter or spring of 1926-7 some of the experimental plants disappeared or were broken. In four of those that remained infection could not be demonstrated in 1927 or subsequently. But in three of them infection was not only evident in 1927, but their inoculated branches bore the first crops of spermogonia and aecia. In every instance the sori were restricted to the needles of 1924, that is, to the needles of the primary infection. Spermogonia appeared first in order and they were followed about a month later by peridermia. From four to eight twigs of the season of 1924 (along with needles of earlier years) had been enclosed in each inoculation tube, and in the case of each of the three successful experiments several of these showed primary infection, but only on needles of 1924.

Final examinations were made in 1928 and in all of the infected twigs referred to above the rust had spread to the needles of 1925, and in two of them to the needles of 1923. Likewise a stimulated growth

TABLE 6. *Milesia polypodophila*—
from *Abies balsamea* to various ferns

(The aeciospores used were from field collections on *Abies balsamea*)

Fern inoculated	Date of inoculation	First observation of uredinia	Date harvested	Results					
				Stages	Location	Total infections	Pinnae Total with lesions	Herb. No.	
<i>Polypodium virginianum</i>	2.viii.24	13.ix.24	13.ix.24	II	Garden	24	—	—	8264
" "	2.viii.24	—	22.vi.25	II	"	—	—	—	—
" "	2.viii.24	13.ix.24	—	II	"	—	—	—	—
" "	2.viii.24	13.ix.24 (lesions only)	13.ix.24	II	"	9	—	—	—
" "	2.viii.24	13.ix.24	13.ix.24	II	"	40	—	—	—
" "	2.viii.24	13.ix.24	13.ix.24	II	"	27	—	—	—
" "	2.viii.24	13.ix.24	13.ix.24	II	"	68	—	—	—
" "	5.viii.24	June 1925	22.vi.25	II	"	—	—	—	8266
" "	5.viii.24	June 1925	22.vi.25	II, III	"	—	—	—	8262(a)
" "	5.viii.24	June 1925	22.vi.25	II, III	"	—	—	—	8262(b)
" "	9.viii.24	June 1925	5.vi.25	II, III	Field	—	13	5	7374(a)
" "	9.viii.24	June 1925	5.vi.25	II	"	—	17	3	7374(b)
" "	9.viii.24	—	5.vi.25	II	"	—	15	6	7374(c)
" "	9.viii.24	—	5.vi.25	II	"	—	21	9	7374(d)
" "	9.viii.24	June 1925	5.vi.25	II, III	"	—	26	13	7374(e)
" "	9.viii.24	15.ix.24 (lesions only)	21.vi.25	II, III	"	41	25	17	7375(a)
" "	9.viii.24	—	21.vi.25	II, III	"	26	23	13	7375(b)
" "	9.viii.24	15.ix.24	15.ix.24	II	"	25	—	—	—
<i>Dryopteris marginalis</i>	4.viii.24	5.vi.25			No infection				
" "	4.viii.24	5.vi.25			" "				
" "	8.viii.24	5.vi.25			" "				
<i>Dryopteris spinulosa intermedia</i>	8.viii.24	5.vi.25			No infection				8260 a
" "	8.viii.24	5.vi.25			" "				8270 a

The "garden" (pot) cultures showed about 200 primary infections; these bore hundreds of uredinia.

The field cultures showed about an equal number of primary infections; these bore hundreds of uredinia.

The frond under number 7375a showed lesions on 17 out of 25 pinnae; these lesions were rich in teliospores and they carried about 155 uredinia, the number per pinna ranging from 1 to 29.

Out of 21 experiments 3 only showed no infection. Many controls were carried and all remained free from infection.

was obvious, so that one could say with certainty that the loose broom, a characteristic phenomenon in trees affected by *M. polypodophila*, was well started. One of these brooms (Herb. no. 8596), representing the entire result of an experiment, was harvested as a unit. It possesses four primary infection areas. Spermogonia and peridermia occur on the needles of 1923 and 1925 as well as on those of 1924 that still remained (several hundreds in all), and infection has plainly spread to the proximal needles of 1926 in many places.

The percentage of infected needles in a given infected branch area is high—commonly from 90 to 95 per cent. The number of peridermia on individual infected needles of the experiments ranged from one to fourteen, and averaged about seven. Some needles on a successfully inoculated twig remain free from primary infection, but most of them, though not necessarily all, eventually are invaded by mycelium that is perennial in the stem. It should be stated that the spread of the fungus from season to season is by means of mycelium that persists in the stem—mycelium that doubtless originated in primary needle lesions. Needles of all ages are susceptible to infection, but needles of the current season only are susceptible to primary infection. The subsequent course of the mycelium is a growing downward into the contiguous stem, and thence through the cortical tissues of the stem upwards and downwards, the mycelium as it advances sending out hyphal branches into uninfected needles of any age through their bases. Usually affected needles fall off during the winter following the summer in which they bear peridermia. It happens at times, however, that some persist, especially those that produce spermogonia only in that year, and in the following year they produce what is potentially or actually a second crop of peridermia.

The field inoculations were made with aeciospores from a collection made on Timagami Island in Lake Timagami, a part of which collection is incorporated in my herbarium under number 7267. The location chosen was Island 1024, a small island distant from known infections and itself free from infected firs. The island is rocky and in the part chosen for the experiments was largely covered by black spruce (*Picea mariana*), white birch (*Betula papyrifera*), a few scattered white pines (*Pinus Strobus*) and a single sapling of balsam fir (*Abies balsamea*). There was a limited number of *Polypodium virginianum* on the floor of the forest—not more than about 100 fronds all told. Each of these was first carefully examined for signs of rust; no traces of rust were found, and those that were not inoculated remained perfectly free from rust at the end of the experimentation. Experiments were set up

on several each of the fronds of eight plants; one of these plants could later not be located; the selected fronds of the remaining seven became infected as a result of the inoculations made.

TABLE 7. *Milesia fructuosa*—
from *Dryopteris intermedia americana* to various species of *Abies*

Fir inoculated	Date of inoculation	First appearance of peridermia	Date harvested	Remarks
<i>A. amabilis</i>	15.vi.33	None	47 days	Very scanty. Spermogonia only.
<i>A. balsamea</i>	5.vi.33	42 days	47 "	Scanty.
" "	12.vi.33	Non-erumpent	50 "	Scanty.
" "	12.vi.33	None	50 "	Scanty. Spermogonia only.
<i>A. cephalonica</i>	24. v.33	35 days (Non-erumpent)	55 "	Scanty.
<i>A. concolor</i>	24. v.33	35 days	48 "	Occasional.
" "	24. v.33	35 "	55 "	Occasional.
" "	1.vi.33	37 "	37 "	Frequent.
" "	1.vi.33	42 "	47 "	Occasional.
" "	12.vi.33	41 "	44 "	Frequent.
<i>A. Fraseri</i>	1.vi.33	40 "	47 "	Frequent. Distorting.
" "	1.vi.33	36 "	36 "	Frequent. Insect eaten.
" "	1.vi.33	36 "	40 "	Frequent. Distorting.
" "	12.vi.33	39 "	40 "	Frequent. Distorting.
" "	12.vi.33	39 "	44 "	Abundant. Distorting.
<i>A. Fraseri</i>				
<i>prostrata</i>	6.vi.33	45 "	46 "	Frequent. Distorting.
" " "	6.vi.33	42 "	42 "	Frequent. Distorting.
" " "	13.vi.33	35 "	35 "	Abundant. Distorting.
" " "	13.vi.33	35 "	39 "	Frequent. Distorting.
" " "	14.vi.33	41 "	42 "	Frequent. Distorting.
" " "	14.vi.33	41 "	42 "	Frequent.
<i>A. magnifica</i>	14.vi.33	37 "	38 "	Very abdt. Very distorting.
" "	14.vi.33	36 "	38 "	Very abdt. Very distorting.
" "	14.vi.33	36 "	38 "	Very abdt. Very distorting.
" "	14.vi.33	34 "	34 "	Abdt. Very distorting.
<i>A. nephrolepis</i>	13.vi.33	42 " (Non-erumpent)	49 "	Scarce.
" "	13.vi.33	38 days	43 "	Occasional.

The scope of the investigation, the positive results of which are recorded, was much more extensive than would appear from Table 7. Two hundred and eighty-four inoculations in all were made on twenty-eight species and eight varieties of *Abies*. The species and varieties on which no infection occurred are not enumerated because the experi-

mental conditions were such that negative results were not interpreted as proof of immunity. Temperatures and moisture conditions were unfavorable for the main part throughout the period of the experiment. From May 24, the date of the first inoculations, up through the end of June the weather was abnormally dry and warm, drying winds were above normal, precipitation meager and relative humidity and cloudiness below normal. The rainfall for the last week in May totalled 0.1 inches, for the entire month of June 1.2 inches and for the first half of July 1.4 inches. Moreover, most of the trees inoculated were unavoidably in exposed situations with the result that more or less drying of the needles took place and in many instances there was some sunscorching of the foliage. The most striking infection was obtained on *Abies magnifica*, and in this instance the trees inoculated were the most protected of all. They are small and are situated in a close copse adjacent to and at the base on the north side of a steep hill covered by a thick stand of hemlocks. The contrast afforded by the scanty, though positive, infection on *Abies balsamea* is particularly worthy of note because this species is the usual haploid host of *M. fructuosa*, and in its natural habitat is often very heavily infected. The trees inoculated in this experiment are small and unprotected on all sides. Measured by these facts it is reasonable to suppose that some at least of the species that remained free from infection would prove susceptible under conditions more favorable to infection.

On the other hand it cannot be assumed that some species of *Abies* may not be immune to *M. fructuosa*, nor that susceptible species differ from one another in their resistance to this rust. As to the latter my experimentation affords grounds for concluding that differences in resistance do exist among the host species. Such is clearly indicated when comparisons are made as between the effects produced by *M. fructuosa* on *Abies balsamea* on the one hand and on *A. Fraseri*, *A. Fraseri prostrata* and *A. magnifica* on the other. *A. balsamea* in nature is often very heavily rusted by *M. fructuosa*, in some instances to the extent that nearly all of the needles of the current season may be rusted, but the infected needles show little evidence of dwarfed growth or distortion. As for the others named and particularly *A. magnifica* checked growth and distortion are pronounced. It is apparent that for *A. magnifica* attacks of *M. fructuosa* might easily be so disastrous as to prove of considerable economic importance in connection with the natural or nursery production of that species.

Since provision had not been made in the experiment for a supply of

plants of the suitable fern host reciprocal inoculations with aeciospores were not made. Admittedly desirable yet under the circumstances such were not necessary to the establishment of the identity of the haploid hosts of *M. fructuosa* because spontaneous infections from this or similar rusts not only did not occur but were practically impossible. It may, therefore, be safely recorded that the following species of *Abies* can serve as hosts for the haploid phase of *M. fructuosa*: *A. amabilis*, *A. balsamea*, *A. cephalonica*, *A. concolor*, *A. Fraseri*, *A. Fraseri prostrata*, *A. magnifica* and *A. nephrolepis*. With respect to geographical distribution of the hosts in their native habitats this list is of added interest because it comprises species of *Abies* from eastern North America, western North America, Europe and Asia.

The reactions of the rust and the various species of *Abies* infected with *M. fructuosa* exhibited some differences. The spermogonia varied somewhat in size and shape; nevertheless they approximated quite closely the spermogonia of the *M. intermedia* form of this species as described (under the erroneous name *Milesia Kriegeriana*) by Hunter (3), and in all instances were clearly distinct from the larger spermogonia of *M. marginalis*. They varied in their distribution on the needles. On all but *Abies magnifica* they were mostly hypophyllous, but in some instances there were occasional epiphyllous spermogonia as well. On *A. magnifica* they were abundantly amphigenous, almost equally distributed on all surfaces. The affected leaves of *A. Fraseri* and *A. Fraseri prostrata* were often more or less deformed; those of *A. magnifica* were much deformed and smaller than normal; those of the other species showed no evident abnormality in size or form. The various morphological phenomena in connection with these infections are being studied in detail by Miss L. M. Hunter.

DEVELOPMENTAL PERIODS

The period of development of the haploid phase on *Abies*, that is, the length of time that elapses between inoculation with basidiospores and the first production of lesions, spermatia and aeciospores respectively, has been partially recorded for eight (seven if *Milesia fructuosa* and *M. intermedia* are the same species) and fully recorded for three of the species of *Milesia* whose complete life histories are known. The data are collated in Table 8.

In the case of each of the species mentioned above the new needles only of *Abies* are liable to infection following inoculation with basidiospores. This cannot be taken to indicate that the older needles are less susceptible; it is more probable that their constant resistance to invasion

TABLE 8

Developmental period of haploid phase of species of *Milesia*

Species of <i>Milesia</i>	Species of <i>Abies</i>	Period up to first appearance of lesions	Period up to first appearance of spermogonia	Period up to first appearance of peridermia
<i>M. Blechni</i>	<i>A. alba</i> } <i>A. cephalonica</i> }	—	36 days. (?)	55 days
<i>M. exigua</i>	<i>A. Mayriana</i> } <i>A. firma</i> } <i>A. sachalinensis</i> }	—	13-20 days, av. (?)	21-28 days, av. (?)
<i>M. jezoensis</i>	<i>A. Mayriana</i>	—	20 days	—
<i>M. Dryopteridis</i>	<i>A. Mayriana</i>	—	38 days	—
<i>M. intermedia</i>	<i>A. balsamea</i>	10-19, av. 14 days	14-21, av. 18 days	32-38, av. 34 days
<i>M. marginalis</i>	<i>A. balsamea</i>	12-21, av. 14 days	18-23, av. 19 days	39-51, av. 43 days
<i>M. polypodophila</i>	<i>A. balsamea</i>	1-2 years	3 years	3 yrs. 1 mo.
<i>M. fructuosa</i>	<i>A. amabilis</i> } <i>A. balsamea</i> } <i>A. cephalonica</i> } <i>A. concolor</i> } <i>A. Fraseri</i> } <i>A. Fraseri</i> } <i>prostrata</i> } <i>A. magnifica</i> } <i>A. nephrolepis</i> }	—	—	35-45, av. 38 days

is due to the nature of the barrier afforded by their maturer cuticles and outer epidermal walls. Evidence in support of these conclusions is furnished from plants occupied by the mycelia of *M. polypodophila*. Although primary infection with this species occurs in young needles of the current season only and never in older needles, yet once infection is established hyphae regularly invade healthy needles of the older ages by passing internally from the stem cortex through the tissues of the petioles out into the laminae. Indeed, it would seem that the protoplasmic resistance of such needles is even less than that of needles of the current season, for while the struggle between the latter and the parasite is continued for two years beyond the year of infection before reproductive organs are formed, it is shorter by one year and possibly in some instances by two years in the case of needles secondarily infected. Protoplasmic resistance apparently wanes with age.

The period of development of the diploid phase on ferns, that is, the length of time that elapses between inoculation with aeciospores or uredospores and the first production of lesions, uredospores and teliospores respectively, cannot as yet be expressed with the same exactness

as for the haploid phase. But observations have been made on a considerable number of species and experimentation conducted with a few. As for the latter some statistical information is available for five species, namely, *M. Blechni*, *M. exigua*, *M. marginalis*, *M. intermedia* and *M. polypodophila*.

Klebahn (7) inoculated *Blechnum Spicant* with aeciospores of *M. Blechni* experimentally produced and found that the developmental period following infection was protracted; inoculations made July 20 showed lesions along in August; no statement was made as to when uredinia appeared. Inoculations made with uredospores in June were followed in about three weeks by uredinia. Kamei (4) made two sowings of aeciospores of *M. exigua* experimentally produced on *Polystichum Braunii* and obtained uredinia in 13 and 17 days respectively. Data on the remaining three species are derived from my own experiments.

Dryopteris marginalis inoculated with experimentally produced aeciospores of *M. marginalis*, in pot cultures, on various dates from August 20 to August 22, 1924 and August 22 to August 27, 1927 showed no external evidences of infection up to September 15, the last date of observation for both years. It is regrettable that observations could not have been continued for a month or six weeks longer, because in spite of many frosty nights in the locality of experimentation from the middle of September onward some fairly temperate weather is experienced until towards the end of October, perhaps warm enough at times to permit further growth of the fungus. It should likewise be noted that lesions on *D. marginalis* caused by *M. marginalis* are very slow in discoloring. It is a common experience to find tendrils of white spores standing out from the inconspicuous uredinia on portions of the frond not perceptibly less green than the unaffected parts. Hence it is not improbable that uredinia were formed before the onset of winter—a fact determinable only by very close examination. However this may have been, the first uredinia we observed in our experimental plants were in May of the following springs. Teliospores developed about one month thereafter. No inoculations were made with uredospores, but I have concluded that the developmental period is much prolonged following natural inoculation on new fronds with uredospores in the spring from uredinia on overwintered fronds. Throughout the summer there is no sign of the rust and not until fall are lesions and uredinia evident. I have never found uredinia on fronds of the current season earlier than September, and even then rather sparsely. The abundant crop is on

overwintered fronds the following spring. The uredospores then begin to emerge in snowy tendrils soon after the fronds are exposed, even before the last traces of snow disappear. The teliospores do not develop until about a month later, that is, until about the time the buds of *Abies* are swelling and opening.

Inoculation experiments with experimentally produced aeciospores of *M. intermedia* from *Abies balsamea* were conducted on *D. spinulosa* and *D. spinulosa intermedia*—all in pot cultures. Inoculations were made August 12 to 14, 1924 and August 16, 1927. Neither lesions nor uredinia were observed up to September 15, the last date of observation for both years. Here again, just as with *M. marginalis*, it is possible that there was further development before winter set in. If so lesions probably became evident, for on both hosts mentioned lesions in nature are in evidence during the fall. It was likewise not known at that time that the teliospores of *M. intermedia* may sometimes develop in the fall on fronds of the current season. All that can be said further is that uredinia did not form at any time on our experimental plants and that teliospores were not located until June of the following springs. All these phenomena were typical of natural occurrences for the same periods.

Coming to *M. polypodophila* a difference in the story is presented. Inoculations were made with aeciospores from field collections on both potted plants of *Polypodium virginianum* in our garden and on undisturbed plants in the forest. These were made at various dates between August 2 and August 9, 1924. In almost every instance lesions were evident by the middle of September, and many of these bore uredinia by September 13. The elapsed period culminating in production of uredospores ranged from 37 to 42 days. In no instance, however, did teliospores develop on the infected fronds until June of the following spring. These phenomena coincide with observations on natural infections whether in infections following aeciospores or uredospores. Uredinia in such cases may occur as early as August, but I have never found teliospores on fronds of the current season. They appear first on overwintered fronds at about the time the buds of *Abies* are swelling and breaking. The data recorded above are summarized and embodied in Table 9.

Any information on the developmental period of the diploid phase of species of *Milesia* on ferns derived from labels that accompany herbarium specimens can at best be little more than suggestive. Such records do indicate, however, that there are considerable differences

TABLE 9

Developmental period of diploid phase of species of *Milesia*

Species of <i>Milesia</i>	Host	Inoculum used and results
<i>M. Blechni</i>	<i>Blechnum Spicant</i>	Aeciospores—protracted development. Uredospores — uredinia in 3 weeks.
<i>M. exigua</i>	<i>Polystichum Braunii</i>	Aeciospores—uredinia in 13 and 17 days.
<i>M. marginalis</i>	<i>Dryopteris marginalis</i>	Aeciospores—no external signs of lesions at end of 24 days; some uredinia may have formed in late fall, but seen first in spring of following year. —teliospores developed in spring of following year.
<i>M. intermedia</i>	<i>Dryopteris spinulosa</i> <i>D. spinulosa intermedia</i>	} Aeciospores—no external signs of lesions at end of 34 days; no uredinia formed at any time. —teliospores developed in spring of following year.
<i>M. polypodophila</i>	<i>Polypodium virginianum</i>	Aeciospores—uredinia in 37 to 42 days. —teliospores developed in spring of following year.

according to the species. The most striking instance of prompt development is afforded by *M. murariae* on *Asplenium Ruta-muraria* in collections from Switzerland; specimens collected as early as June 12 carry a prolific crop of uredinia on the new fronds. This is in striking contrast to *M. fructuosa* on *Dryopteris spinulosa intermedia* in which the earliest production of uredinia occurs in the fall. As intermediates between these two there is a range from early June to late August as illustrated by the series *M. Feurichii*, *M. Blechni*, *M. dilatata*, *M. Scolopendrii*, *M. carpatica*, *M. vogesiaca*, *M. fructuosa* (on *D. spinulosa americana*), *M. Polypodii*, *M. Polystichi* and *M. Kriegeriana*.

HABITS OF SPORE PRODUCTION

(a) SPERMATIA

Some observations were made on the production of spermatia and their period of discharge in connection with my field studies of *M. intermedia*, *M. marginalis* and *M. polypodophila*. As might be inferred from the relatively large size of their spermogonia and the ample protection afforded them by the host tissues spermatia are produced profusely and their discharge is continued over many days. Examinations of these phenomena were made daily with respect to *M. polypodophila*. In this species as in the others there is an outpouring of the spermatia in liquid suspension, but in *M. polypodophila* it is especially copious. When

the weather is humid the liquid spreads over the entire lower surfaces of the needles on which they are borne, and at times it fairly drips from the needles. It is somewhat sticky and sweetish, but no odor was detected. Discharge was found to continue for about thirty days.

The following excerpts from my field notes (4843) in the Timagami Forest Reserve, Ontario, under date June 9, 1924, embodying observations on the spermogonia of *M. polypodophila* and their habit of discharge, present a graphic picture of the spermogonia of *M. polypodophila* and their behavior. "The affected leaves are now moist on the lower surface, films and droplets—due to the active exudation of spermatia and a colorless fluid. A needle (leaf) pressed against a clean dry glass slide leaves an almost continuous smear of spores and liquid. The spores are hyaline, one-celled, cylindrical to ellipsoidal, and occasionally almost rod-shaped. They measure 2.5-3.2 x 3.5-7 μ . The majority are about 3 x 5 μ . The needles along stretches of the axis of the branch (1) continuous with those that bore peridermia last year, (2) or that carried peridermia-bearing needles last year (now fallen off) show many inactive spermogonia. These are greenish-yellow in color with a blackish dot in the center. On the same needles are new spermogonia interspersed with the old ones, on restricted portions of the needles (usually towards their tips) on which areas there are few or no old ones. The new spermogonia are actively discharging; they are slightly discolored (bluish with yellowish tinge) and the central point is moist and not discolored. The affected needles along these stretches of the stem axis are distinctly paler (slightly yellowed) than normal leaves. Contiguous with these stretches are lengths of the axis on which the needles carry new spermogonia only. These needles are scarcely paler than normal needles on their lower surfaces and not paler on their upper. The spermogonia are commonly scattered along the full length of the needles, but are sometimes restricted to limited portions from the bases outward and not extending all the way to the tips. This is especially true of the needles farthest removed from the affected areas of last year. Nearly all of the needles along a given affected stem axis are infected. The length of an axis affected in a given season bears no relation to a season's growth.

"The number of spermogonia on a needle varies from ten to twenty and they are spaced in lineal rows, one on each side of the midrib. Frequently there may be a stoma more or less eccentrically located on the epidermis that covers a spermogonium. This opens wide, the opening with a jagged line of broken cuticle, and through the opening the spermatia are being discharged."

(b) AECIOSPORES

The peridermia of these species with their first apparently mature aeciospores appear in from two weeks to a month after the spermogonia begin their spermatial discharge—an average of 16 days for *M. intermedia*, 24 days for *M. marginalis* and about 30 days for *M. polypodophila*. The peridermia rupture at their apices and discharge of the aeciospores begins. Rupture is delayed for a few days, however, the length of the interval apparently depending to some extent on weather conditions, being shorter when the weather is rainy or when there are heavy dews. The intervals were found to vary from less than a full day to six days for *M. intermedia*, with an average of three days, and from one to eight days for *M. marginalis*, with an average of four days. The discharge of aeciospores is protracted over a comparatively long period of time. For example it has been frequently noted that peridermia of *M. intermedia* formed soon after the middle of August were shedding spores until towards the end of September.

(c) UREDOSPORES

The habits of uredospore production characteristic of Milesian rusts exhibit considerable diversity, as was discovered from comparative observations on various species. An interpretation of the factors underlying the differences manifested is complex, but much of interest could probably be elucidated by experiment. The factors involved are to be sought for in the innate characters of the individual species, the degree of compatibility as between host and parasite, the influence of the host and the influences of moisture and temperature.

Uredospore production from the same frond is usually active over a long period of time, interrupted only during periods of low temperature or drought. To what extent this applies to individual uredinia is uncertain. In some species, as in *M. Blechni* and several tropical forms, it seems to be relatively short as indicated by the circumstance that often many uredinia at the time of gathering are completely empty—sometimes to such an extent that few or no spores can be found in a collection. In others spores can be found in practically all uredinia regardless of age, as in most of the temperate zone species. The length of the time during which uredospores are produced on a frond naturally depends on the promptness with which uredinia are formed on new fronds and the longevity of these fronds after being overwintered. Striking examples of long sporulating periods are afforded by such species as *M. murariae* and *M. polypodophila*. In the former the new

fronds become infected in spring and sporulation is at once abundant; the same fronds are still producing spores copiously a year later side by side with heavily infested new fronds. Sporulation does not begin as early in *M. polypodophila*, but it is active from midsummer onward and continues throughout all of the subsequent year even late into the fall. A remarkable example of suspension of spore production due to drought is found in *M. laeviuscula* on *Polypodium californicum*. Infection must take place in the spring; but during the drought period, which in parts of California where the rust occurs may extend over several months, the fronds and the rust they carry are inactive. With the coming of the winter rains fronds and rust are revived and sporulation begins, to be continued well on into the following spring. An example of a *Milesia* in which the sporulating period is comparatively short is afforded by *M. marginalis*. Uredinia of this species according to my observations do not form until fall on fronds of the current season, and spore production that season is quite limited. The heavy spore discharge takes place the spring following, but it is rarely continued beyond June, and in dry springs the old fronds may die even before there has been normal time for teliospore formation.

Of all species of *Milesia* I have found none quite so perplexing with respect to uredospore production as *M. intermedia*. Widely distributed throughout the range of *Abies balsamea*, a common species the frequency of which is made possible by the almost constant presence everywhere of its fern hosts in coniferous or mixed forests, it seems to have wholly escaped the notice of collectors because of its common habit of omitting uredinia. My finding of *M. intermedia* resulted from a deliberate search for teliospores on *Dryopteris spinulosa intermedia* after having discovered those of *M. marginalis* on *D. marginalis*. Once having found the teliospores the abundance of this rust soon became evident. Yet several years elapsed, though constantly watching for them, before its uredospores were encountered. The uredinia as I first found them were scattered, very small, immersed, very inconspicuous and their spore output was scanty. Collections made previously were again painstakingly examined for uredinia but with negative results. Thus far my collecting had been done in the eastern Provinces of Canada and the two most northeasterly States of the United States. In 1932, however, in the course of collecting trips in the more southerly range of *Abies balsamea* in western Massachusetts and Vermont, I found a rust on varieties of *D. spinulosa*, easily manifest because of the abundance of its closely-studded, conspicuous, though small, pustular ure-

dinia and abundant discharge of white uredospores. The latter so closely resembled those which I had hitherto found so scantily on *D. spinulosa intermedia* as to be practically indistinguishable. Because of the differences in uredinia and in the habits of uredospore production, the rust with abundant uredinia was described under the name *M. fructuosa* and the other under the name *M. intermedia*. Regardless of whether or not both names will stand, a useful purpose has been served in calling attention to a rust that otherwise might be passed over because of a condition so often characterized by the entire omission of uredinia.

For the purpose of obtaining fuller knowledge of *M. fructuosa* and *M. intermedia* I made a special collecting trip to Timagami in northern Ontario, the Green Mountains of Vermont, the Berkshires of Massachusetts and the Adirondacks of New York in the neighborhood of Lake Placid during the middle and latter part of October, 1932. The visits were made at a time when presumably there would be no further growth of the rusts that year. Timagami and the higher elevations of Whiteface Mountain in the Adirondacks were already partly under snow, and all of the localities visited had already experienced killing frosts. The results warranted the efforts made by the extension of our knowledge of distribution, host records, the existence of intergradations of the two "species" and a fuller acquaintance with the habits of teliospore production in *M. intermedia*. To give as complete a picture as possible as a basis for conclusions as to the identity of these species and as a help towards needed further life history experimentation a list of all of my materials of *M. fructuosa* and *M. intermedia* with herbarium numbers and pertinent data is recorded in Table 10.

With these data before us the question arises as to why Milesian uredinia on *Dryopteris spinulosa* and *D. spinulosa intermedia* were not found in Timagami during the years 1924-7, years during which Milesian rusts were being assiduously studied there. I think the correct reply is that if present at all they were rare. The collecting grounds in Timagami were well-defined and were visited often each year. One of these, a small area covered by low-growing *Abies* and interspersed clumps of *Dryopteris spinulosa* and *D. spinulosa intermedia* through the midst of which a trail led was traversed by myself and assistants many times each season. This particular area was one of the best localities for *M. intermedia* both on *Abies* and the ferns, and I repeatedly examined the fronds in search of uredinia; not once were any found. On revisiting the same spot in October, 1932 I found them

TABLE 10

I. *Milesia fructuosa* (continued)A. On *Dryopteris spinulosa* (O. F. Müller) Kuntze

No.	Place	Date	Stages	Age of fronds
10,853	Timagami, Ont.	Oct. 10, 1932	II, III	Current season
10,852a	" "	Oct. 11, 1932	II, III	" "
10,847	" "	Oct. 14, 1932	II, III	" "
10,854	" "	Oct. 14, 1932	II, III	" "
10,859	" "	Oct. 14, 1932	II, III	" "

B. On *Dryopteris spinulosa americana* (Fisch.) Fernald

No.	Place	Date	Stages	Age of fronds
10,668	Mt. Greylock, Mass.	July 14, 1932	II, III	Overwintered (dead)
10,760	" " "	Aug. 7, 1932	II, III	Current season
10,761	" " "	Aug. 7, 1932	II, III	" "
10,761b	" " "	Aug. 7, 1932	II, III	" "
10,883	" " "	Oct. 22, 1932	II, III	" "
10,887*	" " "	Oct. 22, 1932	II, III	" "
10,771	Sherburne Pass, Vt.	Aug. 10, 1932	II, III	" "
10,768*	Whiteface Mt., N. Y.	Aug. 9, 1932	II(rare) III(empty at this date)	Overwintered
10,876*	Whiteface Mt., N. Y. (lowest margin of range of fern)	Oct. 24, 1932	II, III	Current season
10,877*	Whiteface Mt., N. Y. (a protected, sunny exposure, higher up)	Oct. 24, 1932	II(rare) III(abdt.)	" "

C. On *Dryopteris spinulosa fructuosa* (Gilbert) Trudell

No.	Place	Date	Stages	Age of fronds
10,626	Mt. Greylock, Mass.	June 17, 1932	II, III	Overwintered
10,627	" " "	June 17, 1932	II, III	"
10,628	" " "	June 17, 1932	II, III	"
10,764	" " "	Aug. 6, 1932	II	Current season
10,885	" " "	Oct. 22, 1932	II, III	" "
10,886	" " "	Oct. 22, 1932	II, III	" "
10,629	Searsburg, Vermont	June 17, 1932	II, III	Overwintered
10,665	Mt. Mansfield, Vt.	July 15, 1932	II, III	"
10,669	" " "	July 15, 1932	II, III	"

D. On *Dryopteris spinulosa intermedia* (Muhl.) Underw.

No.	Place	Date	Stages	Age of fronds
10,847a	Timagami, Ont.	Oct. 14, 1932	II, III	Current season
10,848	" "	Oct. 14, 1932	II, III	" "
10,851	" "	Oct. 12, 1932	II, III	" "
10,852	" "	Oct. 11, 1932	II, III	" "
10,854a	" "	Oct. 14, 1932	II, III	" "
10,855	" "	Oct. 14, 1932	II, III	" "
10,892	Becket, Mass.	Oct. 21, 1932	II, III	" "
10,888	Sherburne Pass, Vt.	Oct. 22, 1932	II, III	" "
10,889	" " "	Oct. 22, 1932	II, III	" "
10,893	" " "	Oct. 22, 1932	II, III	" "

*Number 10,876 is from the lower margin of range of host. Number 10,877 is from an open sunny exposure higher up and within the main range of the host and everywhere surrounded by "*M. intermedia*." In Numbers 10,768 and 10,877 the II stage is rare.

II. *Milesia intermedia*A. On *Dryopteris spinulosa* (O. F. Müller) Kuntze

No.	Place	Date	Stages	Age of fronds
8,272	Timagami, Ont.	June 5, 1925	III	Overwintered (Cultures in which experimentally produced aeciospores on <i>Abies balsamea</i> of <i>M. intermedia</i> originating on <i>D. spinulosa intermedia</i> were used.)
9,850c	" "	June 30, 1928	III	Overwintered (Cultures, ditto.)
10,915	Gaspé Co., Que.	Sept. 8, 1928	III	Current season

B. On *Dryopteris spinulosa americana* (Fisch.) Fernald

No.	Place	Date	Stages	Age of fronds
10,871*	Whiteface Mt., N. Y.	Oct. 24, 1932	III	Current season
10,875*	" " "	Oct. 24, 1932	III	" "
10,878*	" " "	Oct. 24, 1932	III	" "

C. On *Dryopteris spinulosa intermedia* (Muhl.) Underw.

No.	Place	Date	Stages	Age of fronds
4,871	Timagami, Ont.	June 12, 1924	III	Overwintered
7,371	" "	June 16, 1924	III	"
7,373	" "	June 18, 1924	III	"
8,267	" "	June 5, 1925	III	" (Cultures ditto as under 8272)
8,260	" "	June 5, 1925	III	" "
8,270	" "	June 5, 1925	III	" "
9,850d	" "	June 27, 1928	III	" "
9,924	Mt. Washington, N. H.	July 5, 1931	II*, III	Overwintered
10,670	Becket, Mass.	July 12, 1932	II*, III	"
10,664	Mt. Mansfield, Vt.	July 15, 1932	II*, III	"
10,800	Sherburne Pass, Vt.	Aug. 11, 1932	III	" (fronds dead)
10,880	Lake Placid, N. Y.	Oct. 23, 1932	**	Current season
10,881	Wilmington Notch, N. Y.	Oct. 23, 1932	**	" "

*Prevalent throughout the main range of host and very abundant.

**Mostly just sporeless lesions; a few spores of stages II and III in a few of the oldest lesions found after careful searching, in such cases making decision difficult as to whether the rust should be called *M. fructuosa* or *M. intermedia*.

***Affected fronds of current season found in Maine, Quebec and Nova Scotia bore sporeless lesions only.

abundantly and on practically every affected frond. A few hundred yards farther on, in a narrow swampy valley just on the other side of an intervening hill is the place where the type material of *M. intermedia* was collected. Many hours were spent there springs and falls of 1924-7 in intensive, undivided search of uredinia; none were ever found. Yet in October 1932, though snow had to be kicked away to locate the ferns, several fronds bearing uredinia were uncovered. A

subsequent re-examination of my earlier collections (all on overwintered fronds) made from that particular area confirmed my recorded observations that though teliospores were abundant there were no uredinia. Half a mile eastward is still another locality where, except for a single frond bearing uredinia of the *M. fructuosa* type found in 1926 or 1927 (subsequently lost), nothing but non-uredinial *M. intermedia* had been seen. There, in October 1932 almost every affected frond both of *D. spinulosa* and *D. spinulosa intermedia* bore quantities of the uredinia of *M. fructuosa*.

With the contrasting situation in Timagami, in 1924-7 as compared with the situation in 1932, it is illuminating to refer to the contrasting situations that existed on Mt. Greylock, Mass. and Whiteface Mt., N. Y. in the season of 1932. In the former locality, that is, on Mt. Greylock, spring came earlier, rust developed on *Abies* earlier and fall was later. A rust of the *M. fructuosa* type abounded there from early August onward on fronds of varieties of *D. spinulosa* of the current season, while the *M. intermedia* type was absent. On Whiteface Mt. rust abounded on *D. spinulosa americana* and except in the lower reaches and in sunny exposures farther up the mountain uredinia did not occur. Even where uredinia did occur they formed very late in the season and quite scantily. The trail up Whiteface Mt. from Wilmington (northern side of mountain) traverses a mile or more of terrain covered with *D. spinulosa americana*; the fronds of an enormous number of them in the fall of 1932 were laden with teliospores and without uredinia except as just indicated. In other words the condition of the rust was typical of *M. intermedia*.

A similar parallel existed in 1932 as between Wilmington Notch, N. Y. and Sherburne Pass, Vt. with reference to the rust on *D. spinulosa intermedia*. In Wilmington Notch, for the main part sporeless lesions were present; the fronds entered the winter in the same condition I have so often found to prevail in northern Ontario, Quebec, Nova Scotia and the White Mountains of New Hampshire. At Sherburne Pass, on the other hand, there was an abundance of both pustular uredinia and telia, though they developed later in the season than on *D. spinulosa americana* from the same locality.

One of two explanations of these phenomena is probably correct. Either both *M. fructuosa* and *M. intermedia* occur on *D. spinulosa*, *D. spinulosa americana* and *D. spinulosa intermedia*, varying in relative frequency periodically and locally, or *M. fructuosa* and *M. intermedia* are one and the same species, the production of uredinia potentially

being always possible but actually existent under certain conditions only. From the assembled data even though direct demonstration is lacking, I incline to the latter view.

It might be urged that a compelling argument in favor of regarding *M. intermedia* as a distinct species is the record of *no uredinia* in the six successful cultures recorded above (Table 2). But it is to be borne in mind that since the experiments were conducted out-of-doors the results would have been expected to coincide (as they did) with the occurrences on naturally infected plants in the same territory. Frankly, I suspect that *M. intermedia* is a condition of *M. fructuosa*, a condition characterized by an omission or reduction of uredinia according to environmental influences. This problem and that of biological strains and host preferences afford interesting topics yet to be conclusively investigated.

(d) TELIOSPORES

The first discovery of teliospores of a *Milesia* was made by Magnus (8) in specimens of *Dryopteris spinulosa* affected with *M. Kriegeriana*. They were found on fronds of the current season and it has been fully established that this is the typical habit for that species. Extended acquaintance with other species, however, has revealed the fact that for most of them the teliospores, if known, develop on affected overwintered fronds only. My discovery of this phenomenon resulted from persistent search for teliospores in an ample collection made in early spring of fronds of *Dryopteris marginalis* rich in uredinia-bearing lesions. A prompt examination for teliospores proved fruitless, but that outcome was not regarded as final because under the belief that these spores are rare I thought they might possibly have been overlooked. Hence as the collection was a large one and only a part of it had been overhauled the fronds were placed in a moist chamber to be kept fresh until the search could be completed. About three weeks elapsed before opportunity was afforded to continue the examination; at once, to my astonishment, I found the lesions throughout crowded with teliospores. Immediate reference to plants in the forest revealed that in them also teliosporic production had taken place. The missing clue to the time of occurrence of the III-stage which subsequent observations have shown to be so prevalent in *Milesia* was uncovered. As the periods of teliospore occurrence for the various species have already been published (2) there is no necessity for listing them here.

A point of interest relevant to those species in which teliospores are

formed on fronds of the current season is the question as to when the teliospores are capable of germination. According to Magnus' account of *M. Kriegeriana* the inference is that the teliospores of that species are immediately germinable. Magnus did not state, however, whether or not germination occurs in the fall under natural conditions, nor did he comment on its relative frequency. Obviously if germination does take place abundantly in the fall such a habit would be wasteful because the needles of *Abies* are not susceptible to infection at that season. Dietel (1) in a later communication recounted that he found the teliospores of *M. Kriegeriana* still ungerminated in the early spring on overwintered fronds bearing them, and I have observed the same phenomenon in suitable specimens of that species which have come to my hand. The nearest parallel to Magnus' observation was my finding in early spring before the new needles of *Abies* unfolded quantities of teliospores with empty cells and open germ pores through which basidia had evidently grown in the case of *M. fructuosa* on *D. spinulosa americana* and *D. spinulosa fructuosa*. Under the circumstances it was impossible to know whether germination had taken place the preceding fall or on exceptionally warm days after the snow cover had melted off in the first blush of spring. That the latter is the more likely interpretation is supported by my recent attempts to germinate the teliospores of this species. Materials were collected in October 1932 from the same hosts and in the same locality, teliospores that must have formed sometime between the middle of August and early October. They showed no signs of germination at the time of collection and all attempts to induce germination in the laboratory have ended in failure up to the time of writing (end of December 1932). It is, therefore, reasonable to conclude that as for *M. fructuosa* its teliospores overwinter in a dormant condition and that germination normally first takes place the following spring at about the time the new needles of *Abies* have just expanded.

In conclusion some comments should be offered with respect to the habit of teliospore formation in the species "*M. intermedia*." From the time of my first finding the species I have observed again and again that sporeless lesions in the fall on fronds of the current season was the prevailing phenomenon, while teliospore-bearing lesions was the prevailing condition on the overwintered fronds the following spring in the same localities. These experiences led me to suppose that the teliospores of this species were formed on overwintered fronds only, but recent observations have revealed the fact that they can also be formed

in the fall on fronds of the current season. On examining a collection of supposedly rusted fronds of *D. spinulosa* made in September 1928 in Gaspé, Que., a collection that had been set aside because the lesions bore no uredinia and presumably no teliospores at that season (Faull, no. 10,915), I found that while some of the lesions were sporeless others already contained teliospores of *M. intermedia*. Similar findings came to light in specimens of rusted *D. spinulosa intermedia* made in October 1932 at Lake Placid, N. Y. and Wilmington Notch, N. Y. My conclusion is that the teliospores of *M. intermedia* do form on the fronds of the current season as well as on affected overwintered fronds depending on the earliness of infection and the nature of the environmental conditions.

HOST RESTRICTIONS

All that is known of host restrictions of various species of *Milesia* has already been referred to or indicated elsewhere in this paper so that a brief recapitulation will suffice. The sole data prior to those presented in this paper on the restrictions of the O-I phase have been contributed by Klebahn and Kamei. Klebahn (7) found that *M. Blechni* would not infect *Picea Abies*, but that the two species of *Abies* he tested served equally as hosts. Kamei (4) found that three species of *Abies* tested were susceptible to *M. exigua*. This paper records a wide range of species of *Abies* susceptible to *M. fructuosa* (Table 7).

With reference to fern hosts Klebahn (7) tested *M. Blechni* on *Blechnum Spicant*, *Dryopteris spinulosa* and *Scolopendrium vulgare* and found that the first-named alone gave positive results. In my own experimentation the three species *M. intermedia*, *M. marginalis* and *M. polypodophila* were tried out on several fern species the inoculations being made with aeciospores in each instance. Aeciospores of *M. intermedia* were sown on *Dryopteris spinulosa*, *D. spinulosa intermedia*, *D. marginalis*, *D. cristata*, *D. fragrans* and *Polystichum acrostichoides*. Infection occurred on the first two, but there was no infection on any of the others (Table 2). Aeciospores of *M. marginalis* were sown on *Dryopteris marginalis*, *D. cristata*, *D. fragrans*, *D. spinulosa*, *D. spinulosa intermedia*, *Polypodium virginianum* and *Polystichum acrostichoides*. Infection resulted on *D. marginalis* only (Table 4). Aeciospores of *M. polypodophila* were sown on *Polypodium virginianum*, *Dryopteris marginalis* and *D. spinulosa intermedia* but infection occurred on *P. virginianum* only (Table 6). It may, therefore, be concluded that the diploid phase of these species is closely host restricted. The data assembled from collections of other species indicate like close

host restrictions. It is true there are a few species like *M. vogesiaca* and *M. exigua* in which several species of ferns are found to be susceptible, but always they are of the same genus. Even here it remains to be determined to what extent biological strains more closely restricted still may exist. The one case in which a *Milesia* may infect ferns of more than one genus is that of *M. nervisequa*, a species the exact generic status of which will be open to question until we know for certain whether or not its spores are white in the fresh condition; but to whatever genus it properly belongs its biological entities will remain unknown until comparative inoculations have been made.

ECONOMIC CONSIDERATIONS

So far as I am aware there are no statistical records extant of the amount of losses to firs or ferns caused by species of *Milesia*. As for ferns the economic damage, in America at least, is probably not of much consequence. Whatever injuries there might be would most concern the owners of properties in summer resort regions where native ferns are so universally grown as outdoor ornamentals. According to my observations the damages from Milesian rusts do not compare with the often distressing injuries caused by species of *Uredinopsis*.

As for *Abies* it is conceivable, judging from what I have seen in the forest, and from what I have seen of the severe effects on the foliage of *A. magnifica* in culture experiments (see Table 7 above), that appreciable injury might result in young plantations where infected ferns are in the immediate neighborhood. Certainly it is true that Milesian rusts do affect natural reproduction to a varying extent. The most important species in this connection covering the range of *Abies balsamea* in eastern America, as deduced from my own more or less casual observations on the subject, are *M. polypodophila* and *M. fructuosa* (including *M. intermedia*).

The former induces a broomy growth of firs, involving practically the entire plant if the attack is made when the tree is young, as is usually the case. The resulting growth is unsightly and worthless. Moreover, in such areas not only is the prospective timber value of the firs spoiled but also none of those badly affected ever produce crops of seeds. Of course, such effects are possible only where *Polypodium* is abundant as part of the under-cover.

Undoubtedly *M. fructuosa* (including *M. intermedia*) is of much wider significance in relation to the natural reproduction of the balsam fir, partly because of its wholesale destruction of new needles and because of the general prevalence of its fern hosts. Seedlings on the forest

floor are either killed outright where infection is heavy or greatly retarded in getting a start. Older plants, up to four or five feet in height, sometimes suffer from the loss of an appreciable part of their foliage of the current season. Indeed I have seen areas in eastern America where *Dryopteris spinulosa* or its varieties abounded, in which rust injury almost certainly played a part in reducing the balsam fir as a constituent of the forest stands or in preventing it from becoming as fully established as it otherwise would. This feature in the competitive struggle for existence applies all the more to firs in the southerly limits of their range, that is in regions where ferns most abound and where the firs are subjected to a greater struggle against unfavorably climatic conditions. Reduced in numbers and checked in growth the firs become outgrown and overgrown by other species. It is probably true that such checks to fir reproduction in many of these instances would be considered desirable from the standpoint of forest values. But, however that may be, the fact remains that whenever intensive studies are being conducted for the purpose of quantitatively forecasting forest successions fern rusts as influencing factors should not be disregarded. Plate 86 illustrates the disastrous effect of a fern rust (*Milesia intermedia*) on seedlings of balsam fir growing under natural conditions. The forester should bear in mind the principle that firs and ferns of certain kinds are incompatible neighbors where fern rusts are strongly entrenched.

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SUMMARY

1. Milesian rusts are now known in nature (including a few yet unpublished) to occur on species of about sixteen genera of ferns—all of the family Polypodiaceae—distributed among the polypodiaceous subfamilies Acrosticheae, Aspidieae, Asplenieae, Davallieae, Polypodieae, Pterideae and Woodsieae. They are also known either in nature or cultures on eleven species and one variety of *Abies*, namely, *A. alba*, *A. amabilis*, *A. balsamea*, *A. cephalonica*, *A. concolor*, *A. firma*, *A. Fraseri*, *A. Fraseri prostrata*, *A. magnifica*, *A. Mayriana*, *A. nephrolepis* and *A. sachalinensis*.

2. Hosts of both the haploid and diploid stages in the life histories

are now known for ten species of *Milesia* (nine if *M. fructuosa* and *M. intermedia* are identical), namely, *M. Blechni*, *M. Dryopteridis*, *M. fructuosa*, *M. exigua*, *M. intermedia*, *M. jezoensis*, *M. Kriegeriana* (Mayor, unpublished), *M. marginalis*, *M. Miyabei* and *M. polypodophila*. This paper records the data of life history studies on *M. fructuosa*, *M. intermedia*, *M. marginalis* and *M. polypodophila*.

3. The developmental period of the haploid phase (the phase on *Abies*) of Milesian species varies widely and is approximately constant according to the species. The period up to the first appearance of lesions ranges according to the species from 10 days to 2 years, up to the first appearance of spermogonia from 13 days to 3 years and up to the first appearance of peridermia from 21 days to 3 years 1 month (Table 8). The developmental period of the diploid phase (the phase on ferns) does not show such great differences, but it too varies widely according to species (Table 9).

4. Spermatial discharge is relatively abundant and long continued. The most striking instance is that of *M. polypodophila* for which species it may continue for a month, the spermatial fluid at times fairly dripping from the needles.

Aeciospores make their appearance in from two weeks to a month following the first discharge of spermatia. The period under normal conditions averages about 16 days for *M. intermedia*, 24 days for *M. marginalis* and 30 days for *M. polypodophila*. The discharge of aeciospores may continue over several weeks.

Uredospore production from the same frond is usually active over a long period of time, but there are striking exceptions. Perhaps the most remarkable instance of longevity is afforded by *M. polypodophila*—discharge is known to begin in midsummer and to continue until late in the fall of the subsequent year.

5. Significant variations have been observed in *M. intermedia* as originally defined with respect to the time of formation of teliospores (Table 10, II). Ordinarily these form on *Dryopteris spinulosa* and *D. spinulosa intermedia* throughout most of the localities with which I am familiar in the spring on overwintered fronds, but I have recently discovered that some at times develop in the fall on fronds of the current season.

Equally significant variations have been observed in what I take to be *M. fructuosa* as originally defined with respect to the relative abundance of uredinia (Table 10, I). Ordinarily these occur abundantly on *D. spinulosa americana* and *D. spinulosa fructuosa*; but in the upper

reaches of Whiteface Mountain of the Adirondacks I found on *D. spinulosa americana* a complete lack of them on the majority of affected fronds.

Owing to the absence of sharply cut morphological differences between *M. intermedia* and *M. fructuosa*, the modifications noted above serve to break down clear distinctions between them. My tentative conclusion is that *M. intermedia* and *M. fructuosa* as originally defined refer to different manifestations of the same rust species, manifestations that appear to be determined by host or climatic factors. The name *M. fructuosa* has priority. Its definition then should be amended by stating that uredinia vary in occurrence from none to many, in morphology from few-spored, vesicular, depauperate to many-spored, pustular, fairly conspicuous, and that teliospores form in the fall on fronds of the current season, or in spring on overwintered fronds, or part in the fall and part in the spring.

Pondering on the factors that determine the formation of teliospores in Milesian rusts one thinks of such interesting work as was accomplished by Waters (9) on the subject of this phenomenon in certain other rusts. Waters recorded that for nine species of rusts studied by him teliospore and uredospore formation could be influenced by experimental methods. He stated as part of his summary that teliospores were formed when "the host plants were placed under environmental conditions unfavorable for their development." It will be interesting to learn to what extent the metabolic state of the host determines teliospore formation in Milesian rusts, a state that in some hosts presumably would be attained in the fall, in others in the spring only after the fronds had overwintered. In the absence of direct observation on this point conclusions would be speculative, particularly when we know of such rusts as *Melampsorella Caryophyllacearum* and *Hyalopsora Aspidiotus* in which teliospores form solely in unfolding young leaves in the spring, leaves in which metabolic conditions would appear to be at their best.

6. Teliospores of *M. fructuosa* formed in the fall could not be made to germinate before the onset of winter. Evidently they require a resting period and their natural time for germination is in the following spring at the time the needles of *Abies* are unfolding.

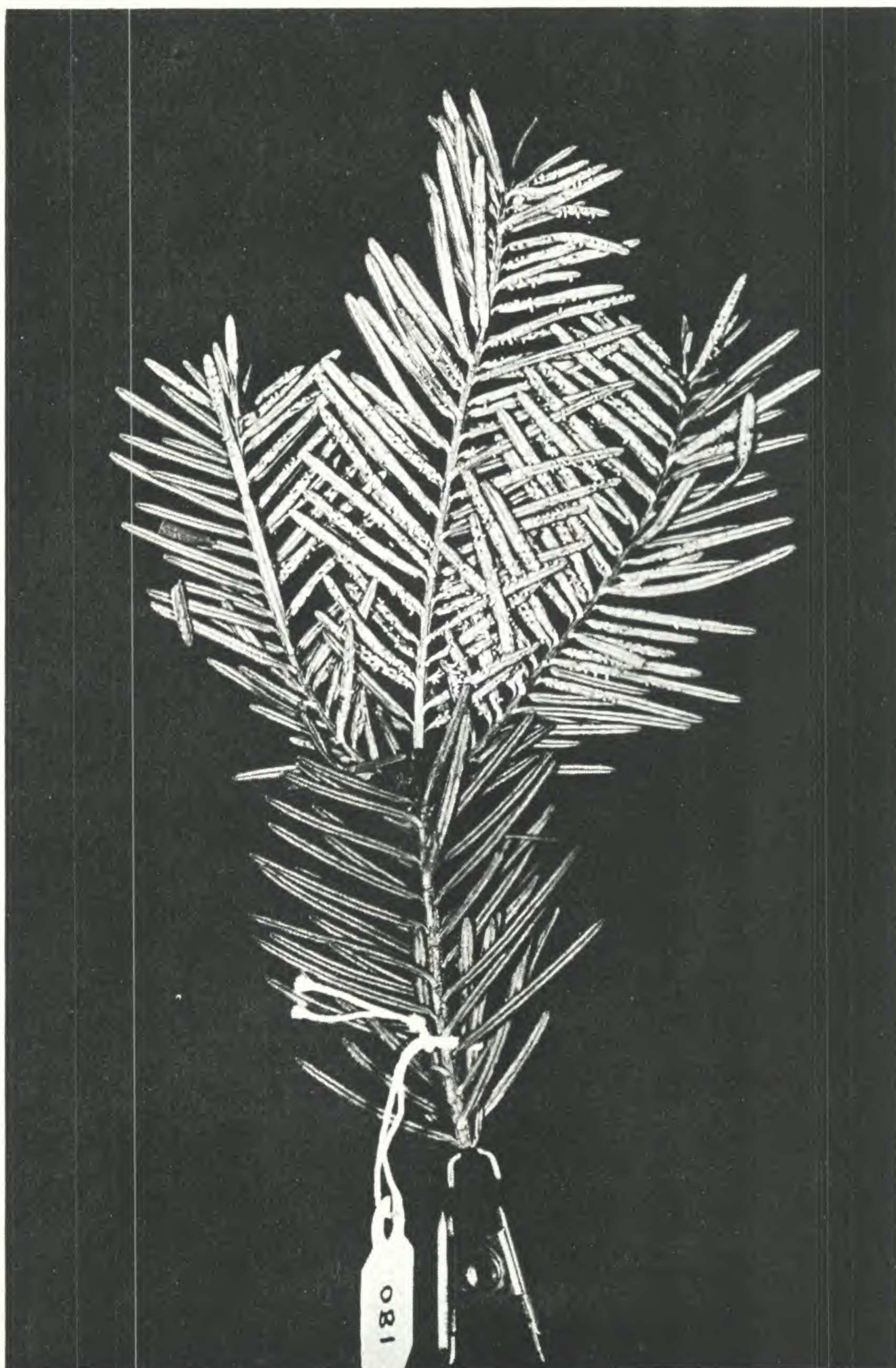
7. Evidence is accumulating that species of *Milesia* are not closely restricted with respect to the species of *Abies* they may infect. This paper records (Table 7) successful inoculations of *M. fructuosa* on *A. amabilis*, *A. balsamea*, *A. cephalonica*, *A. concolor*, *A. Fraseri*, *A. Fra-*

seri prostrata, *A. magnifica* and *A. nephrolepis*—a list of hosts comprised of representatives from eastern North America, western North America, Europe and Asia.

On the other hand evidence is accumulating that species of *Milesia* are much more closely restricted with respect to their fern hosts. This paper records the results of experiments pertaining to this question in which three species were tested each on several species of ferns. (a) *Milesia intermedia* from *Abies balsamea* was inoculated on to *Dryopteris spinulosa*, *D. spinulosa intermedia*, *D. marginalis*, *D. cristata*, *D. fragrans* and *Polystichum acrostichoides*; infection resulted on *D. spinulosa* and *D. spinulosa intermedia* only (Table 2). (b) *M. marginalis* from *Abies balsamea* was inoculated on to *D. marginalis*, *D. cristata*, *D. spinulosa*, *D. spinulosa intermedia*, *Polystichum acrostichoides* and *Polypodium virginianum*; infection resulted on *D. marginalis* only (Table 4). (c) *Milesia polypodophila* from *Abies balsamea* was inoculated on to *Polypodium virginianum*, *Dryopteris marginalis* and *D. spinulosa intermedia*; infection resulted on *P. virginianum* only (Table 6).

8. The reactions of the rust and the various species of *Abies* infected with *M. fructuosa* exhibited some differences. There were slight variations in the size and form of the spermogonia; but the type remained approximately constant. A greater difference was found in the distribution of the spermogonia, particularly on the needles of *Abies magnifica*. In this fir they were strikingly amphigenous, almost equally distributed over all surfaces of the affected needles and not as in the other firs characteristically hypophyllous. The rusted needles of three of the firs showed some distortion, namely, in *A. Fraseri*, *A. Fraseri prostrata* and *A. magnifica*. The greatest effect resulted on *A. magnifica*—marked distortion and dwarfing.

9. Economically certain Milesian rusts are of some importance with respect to the unfavorable effect they exercise on the natural reproduction of *Abies*. *Milesia polypodophila* and *M. fructuosa* are noteworthy examples. The former causes unsightly and worthless plants of *A. balsamea* and the latter may kill or hold in check seedlings and saplings where the balsam fir is associated with rusted ferns. It is apparent from culture experiments that *M. fructuosa* is potentially a menace to young *A. magnifica*. Whenever intensive studies are being conducted in regions in which *Abies* constitutes a part of the forest stand, for the purpose of quantitatively forecasting forest successions, fern rusts as influencing factors should not be disregarded.



BIOLOGY OF MILESIA RUSTS